Basilicus tyrannus (Murchison) and the glabellar structure of asaphid trilobites

R. A. Fortey

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD.

Synopsis

The type species of *Basilicus*, *Asaphus tyrannus* Murchison 1839, is refigured and discussed in relation to *B. peltastes* Salter. Lectotypes are selected. The glabellar structure of this and other Asaphinae suggests that the 'basal glabellar lobes' are of genal origin, beginning as bacculae which are progressively included within the cephalic axis in effaced species. This glabellar structure differs from that of other asaphids, and may be appropriate for the definition of monophyletic subfamilies.

Introduction

Basilicus tyrannus (Murchison 1839) is one of the most familiar British trilobites, represented in every student collection and any museum with Palaeozoic pretensions. It is a curious omission that it has not been given a recent scientific description or ever illustrated photographically, apart from a fragment by Whittard (1964) and some poor material by MacGregor (1963). Jaanusson (*in* Moore 1959: fig. 248, 3) gave a drawing of *B. tyrannus*, and a diagnosis of the genus based upon it. Since I have been studying asaphid trilobites, from Australia, Newfoundland, Spitsbergen and Wales, the problem of classifying this particularly intractable group has raised questions concerning the structure of the asaphid glabella. A redescription of *B. tyrannus* is combined here with some remarks on the construction of asaphid cephalic axes and the definition of the subfamilies in the group.

Glabellar structure of Asaphidae

Most asaphids are more or less effaced, and this involves the loss of visible cephalic segmentation and of definition of axial furrows. Since effacement is an advanced character capable of development in separate subgroups within the Asaphidae (i.e. is manifestly polyphyletic) we cannot base our classification of asaphids on effacement. It is accordingly important to find species or specimens in which the furrows are developed as clearly as possible; a similar problem exists in the Agnostida, among which smooth forms are repeatedly generated.

Jaanusson (*in* Moore 1959: 334–335) defined the subfamily Asaphinae as having an expanded frontal glabellar lobe, and 'lateral glabellar furrows commonly strong, obliquely directed', with a pair of 'lateral glabellar lobes' at the base of the glabella. This interpretation of asaphine morphology has been used in subsequent descriptions of *Asaphus*-like forms (e.g. Dean 1966) and is apparently generally accepted. Here we give a different interpretation. The so-called basal 'lateral glabellar lobes' are regarded as part of the fixed cheeks, inflated bacculae that became effectively incorporated in the axial region in some species. The 1P 'lateral glabellar furrows' are regarded simply as that part of the axial furrow lying between the frontal lobe and the bacculae, which are deepened into apodemes in the 1P position. This is at or near the point of maximum constriction of the glabella. Posteriorly the axial furrows are normally effaced in asaphines, but where they are not they diverge again from the constriction so that the general outline of the glabella is an hourglass-shape. Effacement usually increases with size during ontogeny so that large specimens often have the occipital furrow effaced, for example. In species with the whole posterior part effaced it is impossible to tell which parts of the axial region are of glabellar and which of extra-glabellar origin. In these cases assignment to the subfamily Asaphinae is made

on the characteristic posterior constriction of the glabella behind the frontal lobe. There are several lines of evidence leading to this assessment of glabellar form:

1. Bacculae are commonly developed in asaphids other than asaphines. In these examples there is no doubt about the origin outside the glabella. See, for example, among the Niobinae *Niobella* aff. *imparilimbata* (Tjernvik 1956: pl. 5, fig. 11) and *Gog catillus* Fortey (1975 : pl. 3, fig. 1). However, even in these forms there is a tendency for the furrows separating bacculae from glabella to become effaced, that is, for incorporation of the bacculae into the axial structure; see *Niobella bohlini* Tjernvik (1956 : pl. 5, figs 4, 6).

2. Smaller specimens of *Asaphus* itself (Fig. 1) do not show conspicuous bacculae, but the course of the axial furrows shows up under alcohol. Note that the inner ends of the axial furrows show as a pair of dark patches, which represent thickening of the cuticle as a pair of calluses. These are the 1P apodemes. There is little indication of any cuticle thickening exterior to the axial furrows.

a   b

Fig. 1 *Asaphus* sp. of *expansus* type, mid-part of cephalon, ×5; a, whitened with ammonium chloride to show glabellar tubercle just in front of occipital furrow and general course of axial furrows; b, under alcohol to show thickened patches of exoskeleton representing muscle insertion areas at posterior end of defined axial furrows. Old coll., BM(NH) 42178; Pulkova, Leningrad, Russian platform; Ordovician, Llanvirn.
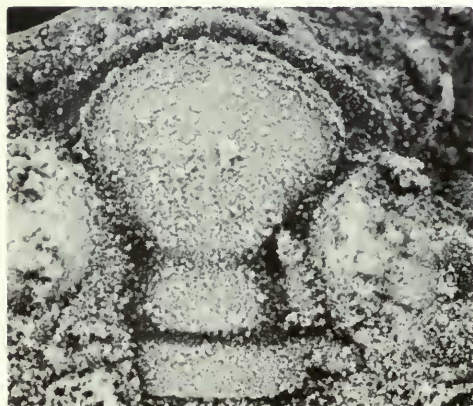

Fig. 2 Asaphid, gen. nov. Latex cast of cranidium preserved as external mould, ×6, showing 1P developed as transglabellar furrow, posterior course of axial furrow defined, and well-developed bacculae adjacent to basal lobe of glabella. Nora Formation, central Queensland, Bureau of Mineral Resources, Canberra, coll.

3. Some anomalous new asaphines from the early Ordovician of Australia have deep dorsal furrows (Fig. 2). In the form illustrated the 1P furrows have become conjoined across the glabella. The furrow defining the inside of the 'basal lobes' runs continuously to the occipital ring, and is not, therefore, effaced in the manner of most Asaphinae. In this case the only reasonable interpretation is that this furrow is axial. The furrow defining the *outside* of the baccula evidently meets the posterior border burrow (and is extra-axial).

4. Where the bacculae (and the adjacent axial furrows) are effaced in large individuals they are present in earlier growth stages. This is true of *Basilicus tyrannus* (Fig. 7, p. 260).

Subfamily classification in asaphids

If the interpretation of the glabella given in the previous section is correct there are implications for the classification of the family (Fig. 3). The fundamental cephalic character separating the Asaphinae from other subfamilies is the glabella with an expanded, often inflated frontal lobe, a posterior constriction at about the level of the palpebral lobes and a backward expansion to the occipital area. Bacculae may or may not be developed, although they usually are in the Arenig and later species, and are incorporated within the axial region to variable degrees. A glabellar
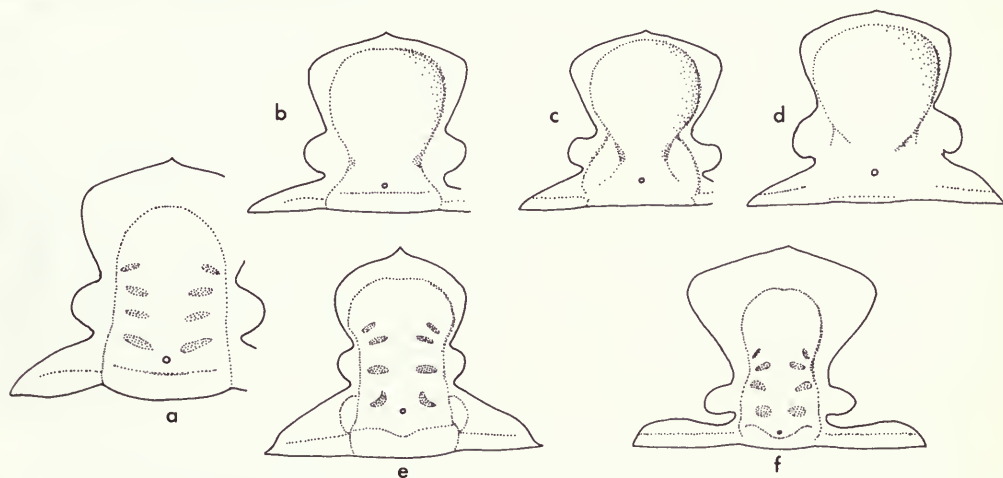

Fig. 3 Schematic diagram showing morphological history of asaphid glabella. 3a, primitive condition, retained apparently in isotelines—see, for example, *Golasaphus* in Shergold (1975 : pl. 56, fig. 7). 3b–d, asaphines tending towards effacement; b, defined, constricted glabella as in *Proasaphus* Balashova, 1966; c, with bacculae at base, cf. Fig. 2, opposite; d, secondarily effaced condition as in *Basilicus* and allied genera. 3e–f, niobine–ogygiocaridine condition; e, *Niobe*; f, *Ogygiocaris* such as *O. sarsi* in which glabellar tubercle and palpebral lobes have moved to a relatively posterior position.

tubercle placed in an immediately preoccipital position was used by Jaanusson (*in* Moore 1959) as one of the defining characters, and this obtains also with the new definition. The 1P apodemes are at or immediately anterior to the glabellar constriction. Under this concept of the subfamily certain genera of Tremadoc age, at first glance quite different in appearance from *Basilicus* and *Asaphus*, should be included within the same subfamily. In particular *Lachnostoma* Ross, 1951, has a glabella of asaphine type. I have observed on a meraspis cranidium of *Lachnostoma latucelsum*[1] Ross, 1951 small swellings alongside the base of the glabella which are apparently not present on larger cranidia. Also *Proasaphus* Balashova, 1966, from the Tremadoc of the Russian Platform, has an extraordinary hourglass-shaped glabella (Balashova 1966 : pl. 2, fig. 6) which cannot be easily explained without adopting the interpretation of glabellar structure given here. The same genus shows a tendency towards a transglabellar 1P, which has been mentioned on the new Australian form (Fig. 2). The origins of the group may lie in such early Tremadocian

[1]For a comparable species, see Evitt 1961 : pl. 117, fig. 23.

forms as *Bellefontia* (particularly see *B. ibexensis* Hintze, 1953: pl. 4, fig. 2), which apparently have the beginnings of posterior glabellar constriction. Early asaphines, such as *Aulacoparia venta* (Hintze 1953), lack a fork in the hypostoma, which is therefore presumably a derived character.

In effaced forms it may be difficult to decide whether the affinities are asaphine or isoteline— but the back end of the frontal lobe of the former is usually defined. Glabellar structure in the latter group tends to be simple rectangular, but there may be some forward taper or expansion. Bacculae seem to be rare or unknown. Small isotelines (Whittington 1941) appear to have a true deep 1P glabellar furrow. In asaphids generally the width and shape of the cephalic and pygidial doublure is highly variable, and may be significant in the definition of genera, but scarcely at a higher taxonomic level. There has been a recent tendency to upgrade some of the old asaphid 'genera' into new subfamilies. Balashova has proposed three such, all based on species from the asaphid radiation on the Russian platform: Ptychopyginae (Balashova 1964), Pseudoasaphinae (Balashova 1969) and Pseudobasilicinae (Balashova 1971). The eponymous genera of the last two have a glabellar structure of asaphine type, and it seems to me extremely unlikely that the forms included within them have a separate status sufficient to warrant sub-familial distinction. *Ptychopyge* and allied genera proposed in Balashova (1964) have prominent nodes on the fixed cheeks just behind the eyes. Since the eyes in this group of species are all very far back, it seems reasonable to regard these nodes as constricted bacculae, and in essentials of glabellar form the Ptychopyginae are asaphine. Balashova may be correct in assuming separate and isolated radiations of the asaphids in the Baltic region, but this is a different matter from regarding each of these as meriting separate subfamilial recognition. The asaphids on each separate plate in the early to middle Ordovician appear to have been undergoing independent radiations (North America–Greenland, Baltic, southern Europe–South America, and Australia) but to dignify each of these with one or more subfamilies would be unwieldy and would also obscure the broader phylogenetic lines in the family.

In summary, there are three types of glabellar structure in Ordovician asaphids: asaphine, isoteline (which appears to be primitive) and niobine. The ogygiocaridine and thysanopygine glabellar structure appears to be fundamentally similar to that of the Niobinae. An unforked hypostoma is primitive, and development of a median notch was presumably independent in Ordovician subfamilies. In some genera assigned to the Ogygiocaridinae (*Ogygiocaris, Ogygio-carella, Merlinia*) a median protrusion was developed rather than a notch. If asaphid classification is to be based on glabellar structure three subfamilies of Ordovician asaphids can be justified: the Asaphinae, Isotelinae and Niobinae (but note that the name Ogygiocaridinae has nomen-clatorial priority over Niobinae and Thysanopyginae), and in addition possibly the Tangyaiinae Lu, 1975. Another subfamily may be necessary to accommodate more or less plesiomorphic Cambrian forms. The subfamily Symphysurininae Kobayashi is not acceptable, because I have evidence that *Symphysurina* is not an asaphid.

Systematic description

Genus *BASILICUS* Salter, 1849[2]

TYPE SPECIES. *Asaphus tyrannus* Murchison 1839.

Basilicus tyrannus (Murchison 1839)
Figs 4–10

SYNONYMY. See Whittard (1964 : 229). The possibility that *B. peltastes* Salter, 1866, is a subjective synonym of *B. tyrannus* is considered below.

LECTOTYPE. Three specimens were figured by Murchison (1839). One of these (pl. 24) was con-sidered as a variety of *tyrannus*, termed *ornata*, and is not available. Of the other two specimens

[2]*Non* M. Oppel 1811 (*Die Ordnungen, Familien und Gattungen der Reptilien . . .* [&c.]: 19. München), which is a misprint for *Basiliscus* Laurenti, 1768 (Reptilia); it is correctly spelled on p. 29 of Oppel's work, though there ascribed to Daudin. Because a misprint has no status in zoological nomenclature, no action is required to conserve *Basilicus* Salter, 1849.
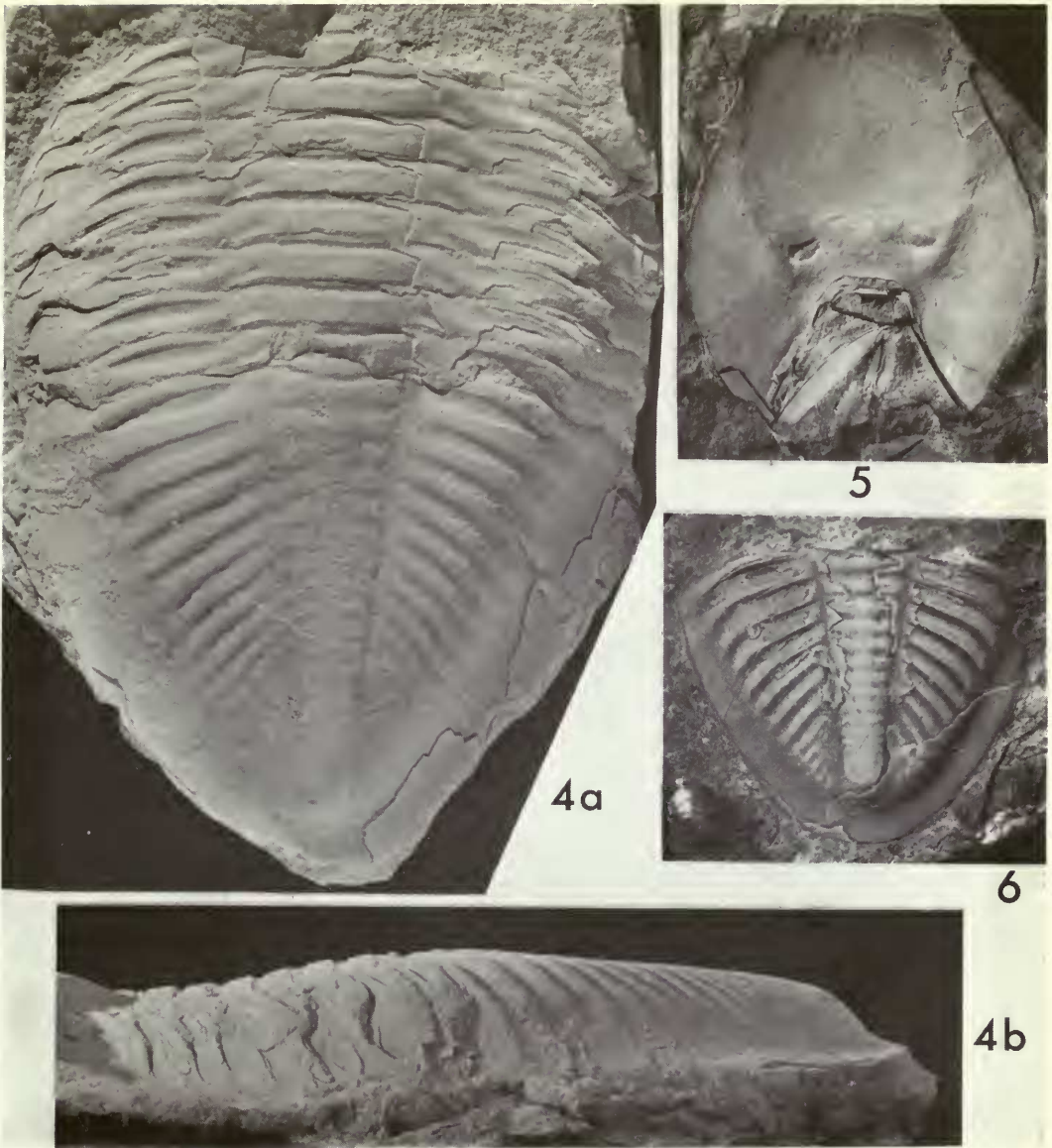
Figs 4–6 *Basilicus tyrannus* (Murchison), ×1. Fig. 4a, b, **lectotype** (herein selected), original of Murchison, 1839; pl. 24, fig. 1B, dorsal and lateral views. Institute of Geological Sciences, Geol. Soc. Coll. 6827. Llandeilo series of Llandilo, south Wales (presumably from Dynevor Park). Fig. 5, ventral view of large, exfoliated hypostoma. BM(NH) It.13227a, same block as originals of Figs 7, 9, 10 (p. 260). Fig. 6, pygidium, smaller than lectotype and with furrows well-developed. BM(NH) I.1312, locality data as lectotype.

the larger (original of Murchison 1839 : pl. 24, fig. 1b), a thorax and pygidium, is here selected as lectotype (IGS Geol. Soc. coll. 6827). Fig. 4.

OCCURRENCE. Williams (1953) gives *B. tyrannus* a stratigraphic range in the Llandeilo district from the Upper Llanvirn to the Lower Llandeilo. The species is only common in this area, being only represented in Shropshire by a few fragments from the Meadowtown beds (Whittard 1964). MacGregor (1963) has illustrated possible *B. tyrannus* from the Berwyn Hills, north Wales. Like most large asaphids with thick cuticles it seems to be a shallow-water form, and presumably
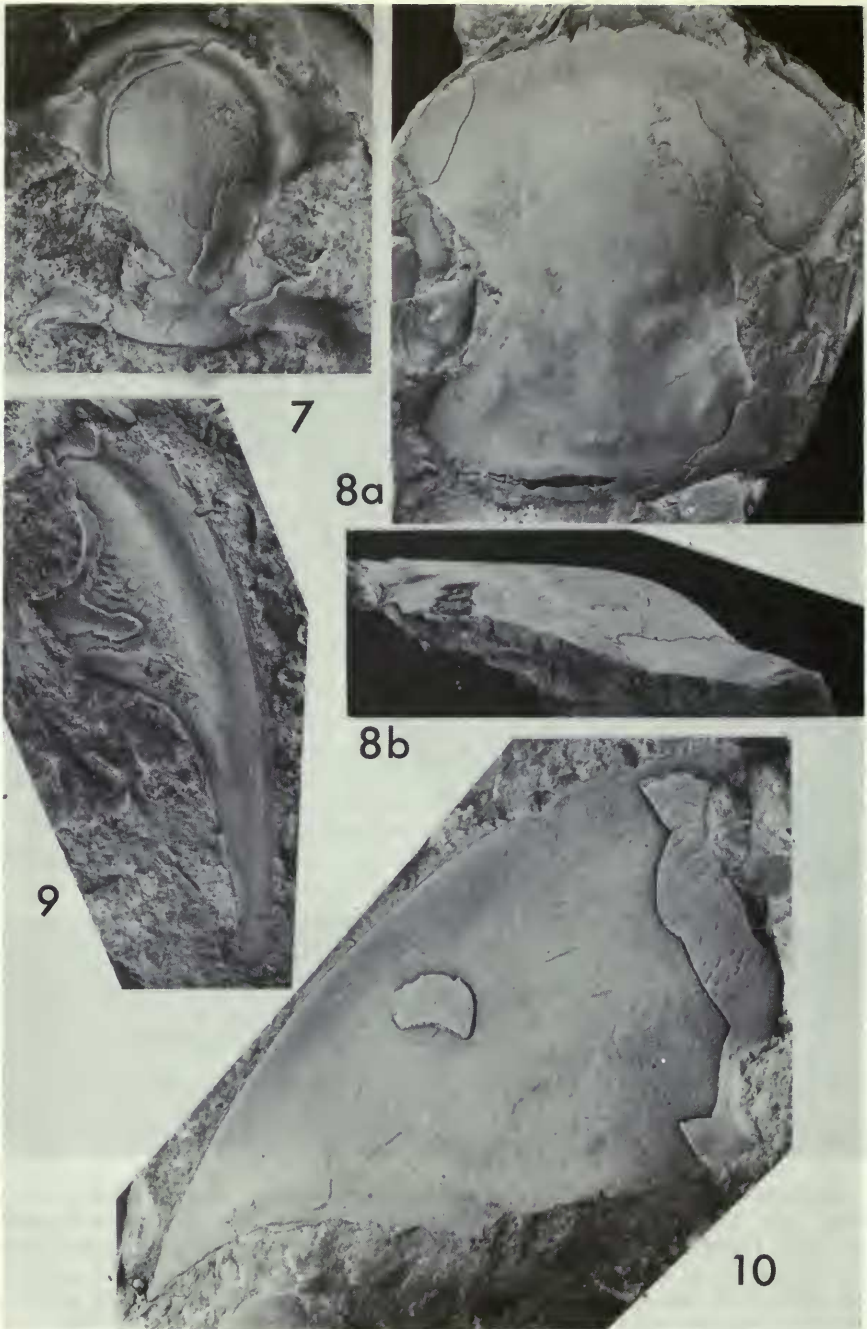
Figs 7–10 *Basilicus tyrannus* (Murchison). Fig. 7, small cranidium, ×2; compare lectotype of *B. peltastes*, Fig. 11. BM(NH) It.13227b. Lower Llandeilo Series, Deer Park track in Dynevor Park, Llandilo, SN 609223. Coll. 1974. Fig. 8, large cranidium in relief, ×1; a, dorsal, and b, lateral view. BM(NH) It.9697. 130 m at 295° from Llan Mill, near Narberth, Dyfed, SN 1433 1394. Fig. 9, small free cheek, ×2; BM(NH) It.13227c, same block as large free cheek, Fig. 10. Fig. 10, large free cheek, ×1; typical of *B. tyrannus*, showing short genal spine compared with Fig. 9. Same bock as Figs 7 and 5. Lower Llandeilo Series, Dynevor Park, Llandilo, by Deer Park track, SN 609223.

its rarity outside south Wales is attributable to a difference in facies. Llandeilo 'flags' with *B. tyrannus* extend westwards to St Clears and Narberth.

COMPARATIVE REMARKS. Salter (1866 : 149–152) gave a good account of this species, and here the purpose is to consider the variation within the species, and the distinctness or otherwise of a second species, *B. peltastes* Salter 1866. As Salter noted, Murchison's variety *ornata* was based on a large specimen, BM(NH) 59785, on which the distinctive surface sculpture of broken and scalloped terrace lines is particularly prominent. The same sculpture is present on smaller specimens, although subdued on pygidia, for example, less than 5 cm long.

Fig. 11   **Lectotype** of *Basilicus peltastes* Salter, selected here, ×1½. Original of Salter 1866 : pl. 22, fig. 1. Note baccula on left. GSM 12793. Llandeilo Series within Dynevor Park, Llandilo.

The large cranidium in relief (Fig. 8) is from Llan Mill, one of Salter's localities for *B. tyrannus*. At this size the bacculae are not distinguishable. Note that what we have termed above the 'frontal lobe' on the glabella in fact shows traces of one pair of depressions, presumably the site of appendage attachment, and so strictly speaking the term frontal lobe should apply to the area in front of these. A small cranidium in relief (Fig. 7) shows a narrower and well-defined border, and the bacculae are distinctly set off from the rest of the glabella in the region adjacent to the eyes, which are proportionately a little longer at this size. This small cranidium occurs on a large block covered with the remains of *B. tyrannus*. The same block has yielded the large hypostoma (Fig. 5), small and large free cheeks (Figs 9, 10) and many pygidia of *tyrannus* type.

The large free cheek, with an ill-defined border and short genal spines, is like those figured by Salter for *B. tyrannus*, but the small cheek has both a better-defined border and relatively long genal spines. These characters were used by Salter (1866 : 152) to distinguish a second species, *Basilicus peltastes*. It now seems possible that some of the supposed differences between *B. tyrannus* and *B. peltastes* can be accounted for by difference in size. The best specimen used to found *B. peltastes* is a relatively small entire exoskeleton (Salter 1866 : pl. 22, fig. 1; Fig. 11 herein). This is here selected **lectotype.** Salter clearly indicated the lateral inflated areas by the glabella that are here interpreted as bacculae, the same features seen on the supposed small *tyrannus* cranidium described previously. It seems that effacement of dorsal cephalic furrows of these asaphids increases with size, and this applies particularly to the posterior part of the glabella and the cephalic border. The same also applies to the large hypostoma (Fig. 5) which has a poorly-defined middle body and longer fork than the smaller specimen figured by Salter. With free cheeks of length about 5 cm it is possible to find examples with genal spines of various lengths; there may have been intraspecific variation in this character at any one size, as well as a decrease in relative size during ontogeny. The largest free cheek of *peltastes* type is GSM 104306.
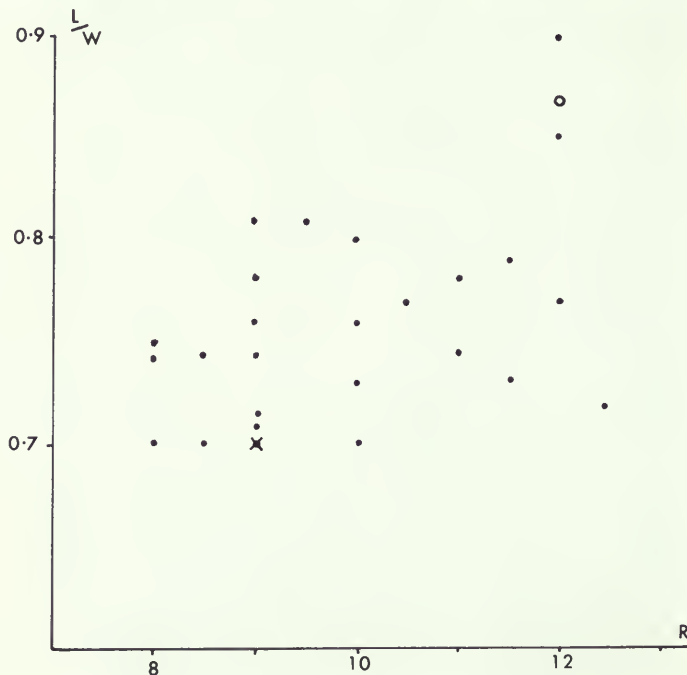

Fig. 12 Graph of length/width ratios of pygidia attributed to *Basilicus tyrannus, sensu lato* against number of pleural ribs, showing broad scatter without discrete grouping. Lectotype of *B. tyrannus* (Fig. 4) is open circle, that of *B. peltastes* (Fig. 11) crossed. Half rib scores obtained when one side of pygidium shows an extra faint rib.

Salter also stressed pygidial differences between *B. peltastes* and *B. tyrannus*, quoting up to 20 axial rings and 12 pairs of ribs on the latter, as against 14–15 axial rings and 9, 10 or rarely 11 pairs of ribs on the former. Counting axial rings or pleural ribs is always problematic, because the posterior ones are invariably faint. On well-preserved specimens of *Basilicus* retaining cuticle there is nearly always a posterior smooth area adjacent to the end of the axis where no ribs are visible. Nine or ten ribs are usually discernable anterior to this area. On some decorticated specimens the most posterior ribs are visible, and these are the ones with as many as twelve (Fig. 6). The best-preserved specimens of pygidia of *Basilicus* from south Wales in the IGS, BM(NH), Sedgwick Museum (Cambridge) and National Museum of Wales show considerable variation in the number of ribs, but 9–10 predominate (Fig. 12). There is no clear break between specimens

referred by Salter to *peltastes* and the rest of the *Basilicus* specimens (usually determined as *tyrannus*). Nor does there appear to be any obvious correlation between length/width ratio and number of ribs. Specimens preserved in silty beds usually have the pleural furrows overdeepened. I have been unable to observe more than 17 axial rings on these specimens, and on specimens preserving cuticle there may be as few as nine clearly defined. It seems possible that Salter was confusing annulation with the prominent transverse terracing at the tip of the axis. Smallest pygidia of *B. tyrannus* are about 1 cm long; these are more transverse than larger ones (length/width ratio 0·6–0·7), similar to *Basiliella*.

In summary, it seems that the differences between *B. tyrannus* and *B. peltastes* can be accounted for by ontogenetic changes, or by variation within the population of a single species (*B. tyrannus*). Ontogenetic changes include loss of bacculae and effacement of the posterior cephalic axial furrows. There may yet prove to be changes in the proportions of the population as a whole through the Llandeilo series; for example, the longer pygidia with 12 ribs may prove to be more abundant at higher horizons. This would require statistical examination of precisely localized collections, which are not yet available.

Acknowledgements

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